

A LOWER CAMBRIAN CORAL FROM SOUTH AUSTRALIA

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ABSTRACT. A Lower Cambrian coral, *Moorowipora chamberensis*, occurs in the Botomian Moorowie Formation near Moorowie Mine in the northern Flinders Ranges, South Australia. The coralla available for study are cerioid, with tripartite cerioid walls characterized by fibrous crystallites belonging to each corallite, separated by dark, fine-grained carbonate. The corallites were built by true individuals (polyps), as evidenced by their contraction to rounded form when clastic sediment was present within the corallum. Tabulae are present, formed as a basal thin, dark layer and upper fibrous layer perpendicular to the upper surface of the plate. The cerioid colonial form with typical coralline wall structure, the presence of short septal spines, the reaction of corallites to influxes of clastic sediment and the construction of the tabulae all indicate that this Lower Cambrian coral may be placed within the anthozoan Subclass Tabulata, albeit with a question mark. This would extend the range of the group considerably.

THE early Cambrian was a time of extensive reef growth, up to the Toyonian or latest early Cambrian extinction. It has been hypothesized that reefs prior to this extinction were constructed principally by archaeocyaths and calcimicrobes (calcareous cyanobacteria), with stromatolite-forming organisms assuming a subordinate role (Rowland and Gangloff 1988). These early, metazoan-dominated ecosystems display many of the features commonly associated with younger Palaeozoic reefs including community zonation, growth into normal wavebase (Rowland 1984; Rowland and Gangloff 1988), and growth interactions that suggest spatial competition. The decline in reef development following the early Cambrian has been attributed to the extinction of archaeocyaths (Copper 1989; Debrenne 1991). It has been presumed that prolific reef growth was not renewed until a new group of preadapted framebuilders evolved, and that this did not occur until Ordovician time, with the first appearance of bryozoans and corals (Sheehan 1985; Copper 1989).

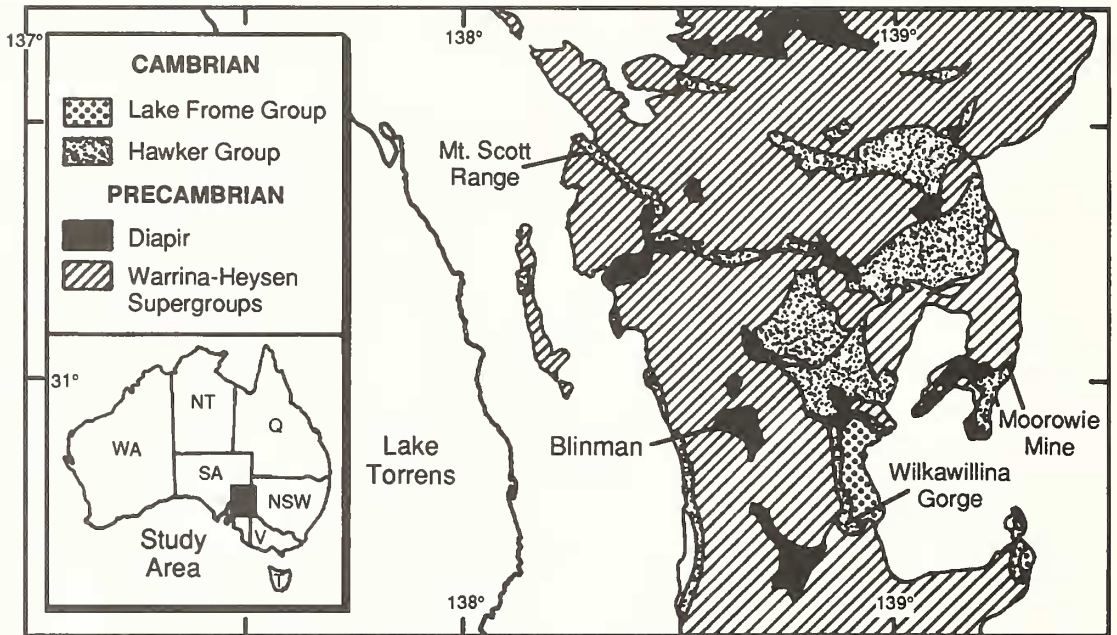
Recent fossil finds in Lower Cambrian strata, however, challenge this common assumption. Two species which may have cnidarian affinities have been reported from reefs in the Botomian Moorowie Formation of South Australia (Lafuste *et al.* 1991; Savarese *et al.* 1993; Fuller and Jenkins 1994). If either of these are genuine tabulate corals, the clade of early Ordovician (Tremadoc, Ibexian) and later Palaeozoic reef corals would have existed prior to the latest early Cambrian (Toyonian) extinction. Alternatively, if these fossils do not belong to the Tabulata, but are cnidarians with skeletal morphologies convergent on tabulate corals, then they represent another group of early Cambrian reef dwellers that went extinct together with the archaeocyaths.

Regardless of their phylogenetic affinity, the two species *Flindersipora bowmani* Lafuste *in* Lafuste *et al.* 1991 and *Moorowipora chamberensis* Fuller and Jenkins, 1994 are significant framebuilding components of Botomian reefs in South Australia. The former, in particular, is a common constituent of Moorowie Formation reefs and is found both as an encruster-binder and as a substrate for attachment by calcimicrobes and archaeocyaths (Lafuste *et al.* 1991; Savarese *et al.* 1993). This paper provides evidence from and further discussion of *M. chamberensis*, which we suggest possesses enough characters diagnostic of tabulate corals to be considered as such, although not unquestionably so. On the other hand, *F. bowmani* has some features in common with corals, but others that question its taxonomic assignment to the Tabulata. We also believe that, as more detailed studies are completed on Lower Cambrian reefs of Australia and correlative reef-bearing

strata in other areas, such as the Cordilleran Region of western North America and the Siberian Platform, other coral discoveries will be made (e.g. Pratt 1991).

LOWER CAMBRIAN REEFS OF THE FLINDERS RANGES

Reefs bearing coral-like skeletons occur within the Lower Cambrian Botomian Moorowie Formation and its equivalents in the Flinders Ranges of South Australia (Text-figs 1–2); some of

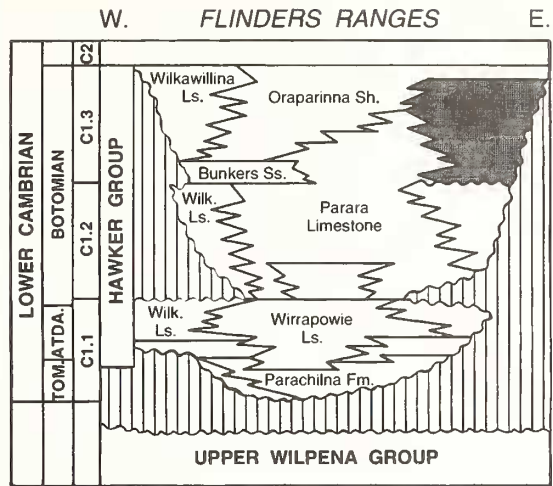


TEXT-FIG. 1. Index map showing location of northern Flinders Ranges within South Australia and location of the Moorowie Mine at the eastern edge of the ranges. Modified from James and Gravestock (1990, fig. 2).

these have been described in detail by James and Gravestock (1990). The Moorowie Formation is geographically limited, and was deposited during the transgressive and highstand phases of the sequence (Gravestock and Hibburt 1991). It is chronostratigraphically equivalent to reef-bearing units elsewhere in the Flinders and Mount Scott Ranges (e.g. the Upper Wilkawillina and Ajax Limestones) and to the Oraparinna Shale (Text-fig. 2). Sediment deposition was influenced by localized synsedimentary tectonics involving diapirism (Coats 1973). Siliciclastic compositions within the Moorowie Formation vary considerably and include red siltstones and mudstones, quartz arenites, coarse arkosic and lithic sandstones, as well as coarse polymict breccias. Associated with these breccias are reefal carbonates including framework boundstones, rudstones, and grainstones. Fossil material discussed here was collected from several levels within the Moorowie Formation at a number of sites located west and south-west of the old Moorowie Mine (Text-fig. 1).

Palaeoenvironmental interpretation of the Moorowie Formation has been treated at greater length by Savarese *et al.* (1993). The hundred metres of exposed strata (Text-fig. 3) represent a non-

TEXT-FIG. 2. Correlation chart of Lower Cambrian, Botomian strata belonging to the Hawker Group, for the Arrowie Basin (Mount Scott eastward to the Moorowie–Yalkalpo Syncline). Simplified from Gravestock and Hibbert (1991, fig. 4).



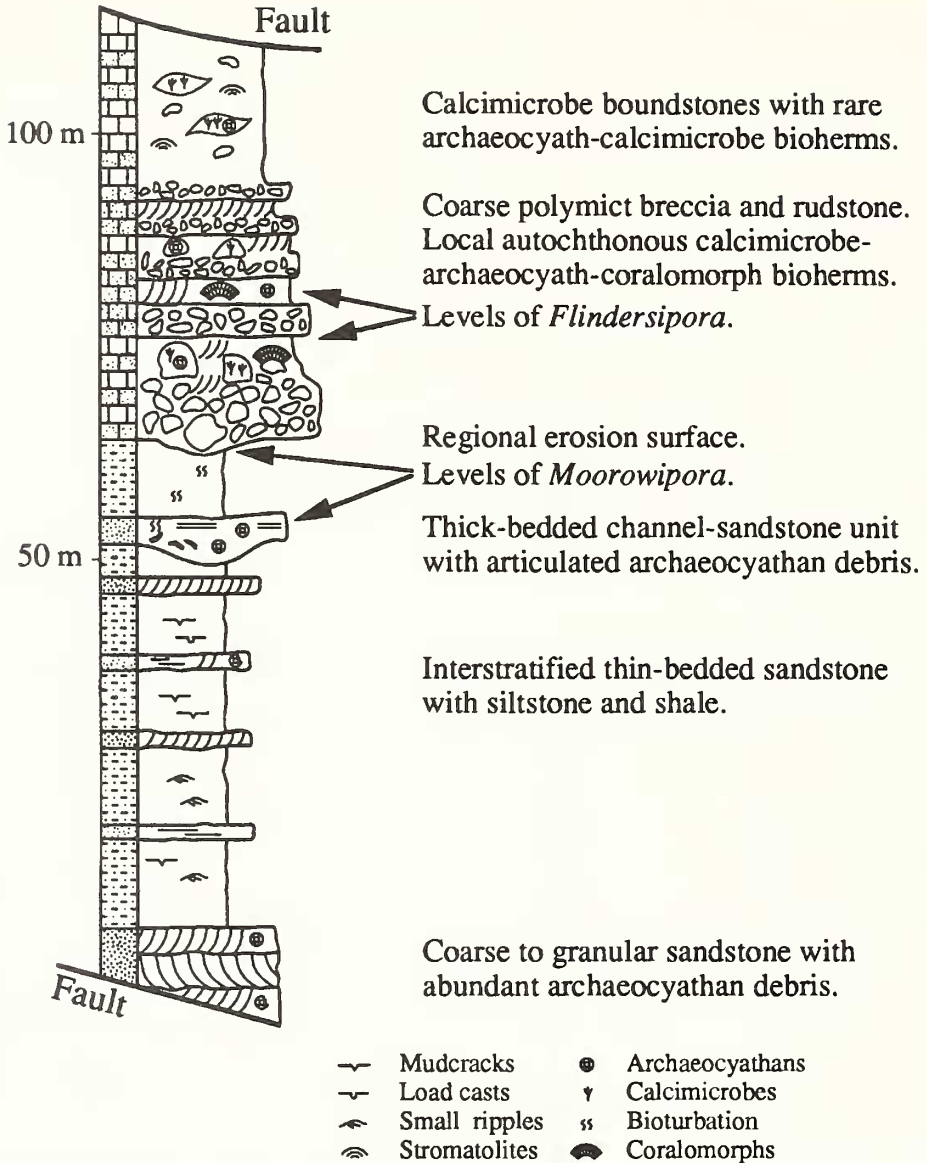
marine to marine transition at the margin of a young seaway. The upper half of the section is composed of interbedded polymict breccias, arkosic, and lithic and quartz arenites which contain marine body and trace fossils and reefal carbonates. The sandstones and breccias are commonly found filling channels. Stratigraphical and sedimentological relationships suggest that these upper strata represent alluvium shed from neighbouring mountain ranges that prograded into the seaway. These deposits have analogues in modern extensional basins and have been called sea-marginal fans (Friedman 1988).

Reef development was founded on these submarine alluvial fans. Alluvial breccias provided a coarse, but stable foundation upon which incipient reef growth could occur during times of sedimentary quiescence. Sedimentation events, if infrequent, did not cause cessation of reef development. Similar sedimentary settings with reef growth have been described from the modern Gulf of Aqaba and Red Sea (Epstein and Friedman 1983; Friedman 1988; Roberts and Murray 1988). Complicating the palaeoenvironmental interpretation of the Moorowie Formation is the presence of reworked reefal carbonates (Text-fig. 3). While some boundstones are clearly autochthonous, others are boulders transported by subsequent alluviation.

The boundstones contain a diverse assemblage of frame-building organisms, with archaeocyaths and the calcimicrobe *Epiphyton* being the most common. Two other calcimicrobes occur, *Renalcis* and *Girvanella*. In addition, stromatolites and sphinctozoan sponges are found, although rarely. Of the coralomorphs, *Flindersipora bowmani* is common (Lafuste *et al.* 1991; Savarese *et al.* 1993). Our discussion of *Moorowipora chamberensis* is based on a beautifully preserved specimen collected in 1992, illustrated by Savarese *et al.* (1993) and herein, and on preliminary study of more than 25 specimens collected in the Moorowie area during August, 1994. The above-mentioned frame-builders occur in complex growth interrelationships (Savarese and Bucklin 1992; Wood *et al.* 1992; Savarese *et al.* 1993), suggesting that competition for space was great on these reefs, as it is on modern ones.

CAMBRIAN SKELETAL CNIDARIANS

Cambrian skeletal cnidarians and the origin of the Palaeozoic corals have been summarized by Scrutton (1979, 1984) and by Jell (1984). Their lists of Cambrian fossils include all that have been regarded as formed by corals (the term is here used in the sense of anthozoans with skeleton-forming capabilities). No Lower Cambrian fossils were recognized by either worker as corals specifically belonging to the two principal Palaeozoic groups, the Rugosa and Tabulata. Scrutton (1979, p. 178) used the term 'coralline zoantharians' while Jell (1984, p. 107) suggested that all of the Cambrian



TEXT-FIG. 3. Stratigraphical section of the Moorowie Formation at Moorowie Mine, South Australia. The sequence is fault-bounded, but provides more than 100 m of strata. Modified from Savarese *et al.* 1993, fig. 1.

forms be grouped under the category he named Coralomorpha, rather than using existing groups within the Cnidaria. We agree with Scrutton that all genera (except *Tabuloconus*) described from Lower Cambrian strata prior to 1979 are best referred to as 'putative corals'. Zhuravlev *et al.* (1993) summarized the types of skeletal microstructures that they observed in a number of genera of Cambrian coral-like skeletons, and proposed paths of diversification of this Lower Cambrian fauna. Several other developments have also occurred since Scrutton and Jell published their reviews, and we discuss these and their relevance to the origin and evolution of the skeleton-forming members of the Phylum Cnidaria, Class Anthozoa.

Tabuloconus kordae Handfield from the Lower Cambrian of British Columbia and Alaska was

described in detail by Debrenne *et al.* (1987) who clarified the morphology and skeletal microstructure of this anthozoan. Corallites in *Tabuloconus* contain tabulae with a skeletal structure consisting of a basal dark layer and an overlying lighter-coloured fibrous layer (as does *Moorowipora chamberensis* but with a wall structure containing 'different types of microstructural units' (Debrenne *et al.* 1987, p. 5)). These authors found skeletal structures in the walls composed of granular, irregular or fibrous crystals, and, believing that all were biogenic, considered that skeletal secretion in *Tabuloconus* was varied and elaborate. These complications of the skeletal structure are here regarded as most likely to have resulted from diagenetic alteration. We would expect that, when well preserved, the fibrous structure would prove to be original, with crystallites oriented perpendicular to the wall surface. This would suggest a close relationship to *M. chamberensis*, also characterized by this type of fibrous wall structure. The Tabuloconidae (Debrenne *et al.* 1987) then may include this species, but at the present stage of research its familial placement is uncertain.

Of the two species of coral-like fossils from the Moorowie Formation known at present, *Flindersipora bowmani* Lafuste was described fully by Lafuste *et al.* (1991) and discussed by Zhuravlev *et al.* (1993), and *Moorowipora chamberensis* is discussed below. We agree with Scrutton (1992, p. 29) in regarding *Flindersipora* as representing at most an early, somewhat atypical coral-like cnidarian that does not fit well into the Tabulata. However, we regard *M. chamberensis* as having a tabulate coral morphology and place it among the tabulates with reservation, because of the long gap in geological record (Lower Cambrian to Lower Ordovician) between it and the oldest definitive tabulates, as expressed below.

Our specimens of *F. bowmani* fit Lafuste's description very closely. Corallite diameters average 2.5 to 3.0 mm, although sizes are diverse; some were undergoing reproductive fission and are therefore enlarged. Although Lafuste placed the species in the Tabulata, Scrutton (1992, p. 29) referred to it as a 'new Lower Cambrian coralline organism', and rejected both its placement in the tabulates and a common ancestry for the two. Likewise we reject its placement in the Tabulata. The most controversial aspects are the wall and septal structure and the manner of budding. The wall and the plate-like septa have identical skeletal structure, each composed of transverse crystallite fibres; this is different from known skeletal microstructures in tabulate corals. There is no development of a tabulate-like cerioid wall separating individuals within colonies. Septa are apparently present, but their internal structure does not resemble that of septa in Rugosa, or the septal spines of Tabulata. Budding in *Flindersipora*, called fissiparous by Lafuste in Lafuste *et al.* (1991, p. 710), consists of splitting of tubules to form new individuals, each of roughly equal size. The new wall dividing them forms as an outgrowth from the septa, which extends across the axis of the individual to join. Fissiparous division is not characteristic of either tabulate or rugose corals (with the exception of the Tetradiidae, which we feel may not belong within the Tabulata).

The geological record does not contain any *Flindersipora*-like skeletons of younger age. Thus, remarks by Lafuste (in Lafuste *et al.* 1991) on the necessity of rethinking the origins and original characteristics of the Tabulata apparently are unwarranted, as *F. bowmani* seems to be far removed from any direct line of descent leading to the tabulate corals (as observed by Scrutton 1992, p. 31). It should also be stated that Zhuravlev *et al.* (1993, p. 369) noted that no ancestor for the later corals could be recognized among Lower Cambrian coral-like fossils, thus suggesting that they did not consider *Flindersipora* as a true tabulate.

SYSTEMATIC PALAEOONTOLOGY

Subclass TABULATA?

Family Uncertain

Genus MOOROWIPORA Fuller and Jenkins, 1994

Type species. By original designation; *Moorowipora chamberensis*, Lower Cambrian, northern Flinders Ranges, South Australia

Diagnosis. Small cerioid colonies with complete tabulae, but no mural pores; corallite diameters average from 3.4 to 4.3 mm; corallites generally polygonal, but some are rounded; colonial form may approach subcerioid during part of lifespan; walls fibrous and prismatic in structure, with three layers present, tabulae with dark line at base of structure, overlain by a fibro-normal layer. Spinose projections from walls and from upper surface of tabulae are present; thus there is a suggestion of septal spines as in later tabulate corals.

Moorowipora chamberensis Fuller and Jenkins, 1994

Plate 1, figures 1–5; Plate 2, figures 1–4; Text-figures 4–5

1993 Undescribed coral; Savarese *et al.*, p. 918, fig. 2D, F.

1994 *Moorowipora chamberensis* Fuller and Jenkins, p. 231, figs 2–7.

Holotype. Museum of South Australia, Adelaide, P34165; from the Lower Cambrian, Botomian, Moorowie Formation, Flinders Ranges, South Australia.

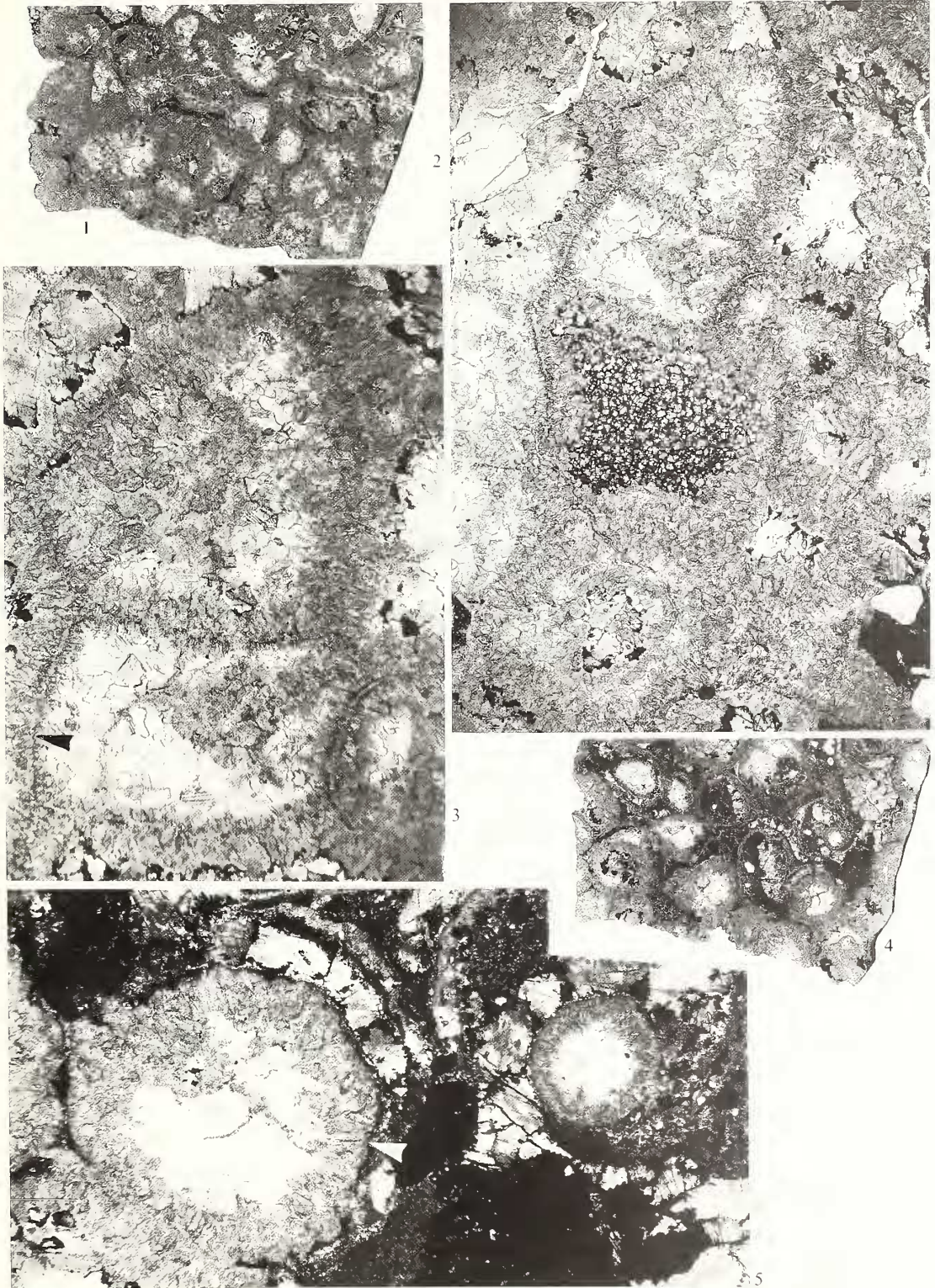
Material. The specimen described herein (Museum of South Australia, P34794) is from the Moorowie Formation, Moorowie Mine, South Australia, less than 2 m from a small bioherm (locality: map coordinate UL343707, Arrowie 1:50000 Sheet, map no. 67736-2, Dept of Lands, Government of South Australia, 1987). Five thin sections have been made from this corallum, three transverse and two longitudinal, which are deposited together with all remnants of the colony in the Museum of South Australia, Adelaide, South Australia. More than 25 additional specimens collected subsequently from several levels within the Moorowie Formation (from channel-form lithic sandstones lateral to small bioherms within the medial portion, as well as from the bioherms themselves) in a 10–12 km square area west and south-west of the old Moorowie Mine. Preservation of skeletal microstructure in these specimens is unfortunately not as good as that in the described colony.

Diagnosis. Cerioid to subcerioid species; small corallum with polygonal corallites having diameters averaging 3.4 to 4.3 mm and thick, three-layered walls with variably developed septal spines, commonly lacking any; no mural pores present; tabulae complete with basal dark skeletal layer and overlying thick fibrous layer.

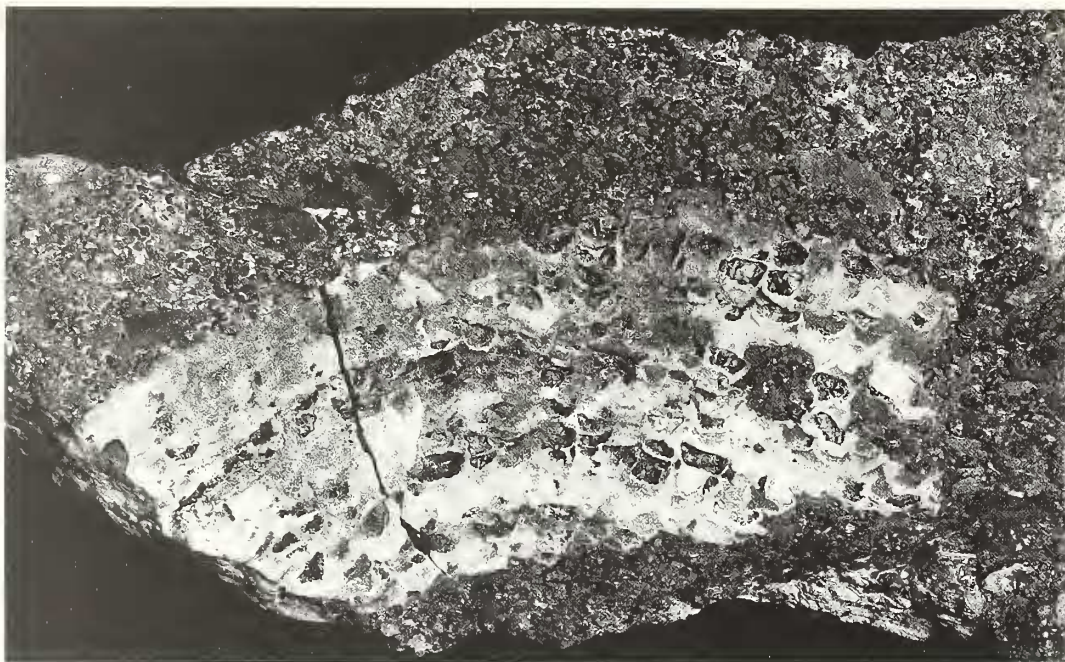
Description. The best preserved corallum measured approximately 120 mm by 55 mm prior to cutting for thin sections. It was found resting on its side within red calcareous wackestone with abundant haematite-coated, well-rounded quartz grains and rock fragments (Text-fig. 4), and is the specimen figured by Savarese *et al.* (1993, p. 918, fig. D, F). Red silt- and sand-sized sediment is found at several levels within this coral. In transverse section (Pl. 1, figs 1, 4), the corallites appear irregularly polygonal, four- to six-sided, with sides of unequal length. Mature sediment-filled calices from the uppermost part of the corallum are irregularly six-sided, with average corallite diameters (average of maximum and minimum diameters) ranging from 3.0 to 4.3 mm in the cerioid portions of these colonies. Subcerioid, rounded corallites, with sediment surrounding them, are smaller, with average diameters ranging from 2.75 to 4.1 mm. Walls are very thick, ranging from 0.6 to 1.66 mm in total thickness in cerioid corallites (Pl. 1, fig. 2). Wall structure is clearly cerioid: three layers consisting of a fibrous wall (or stereozone) preserved on both sides of the central, finer-grained epitheca (Pl. 1, fig. 3). Where sediment has invaded the colony, corallites are round, and walls are much thinner than in

EXPLANATION OF PLATE 1

Figs 1–5. *Moorowipora chamberensis*; all transverse sections; S.A.M. P34794. 1, overview illustrating cerioid nature of corallum; $\times 2$. 2, thick, fibrous walls between corallites and sediment infilled calice in large corallite; $\times 6$. 3, cerioid walls between corallites, each consisting of central dense layer with fibronormal peripheral stereozone on each side (arrow); $\times 10$. 4, overview of portion of corallum with incursion of sediment causing contraction of individual corallites; $\times 2$. 5, enlarged view showing contraction of individuals where in contact with clastic sediment to form smaller diameter, round corallites (arrow); $\times 10$.



SORAUf and SAVARESE, *Morowipora chamberensis*



TEXT-FIG. 4. *Moorowipora chamberensis* Fuller and Jenkins, 1994; S.A.M. P34794; external longitudinal view of specimen prior to sectioning, showing the distinct corallites and sturdy tabulae; $\times 3.3$.

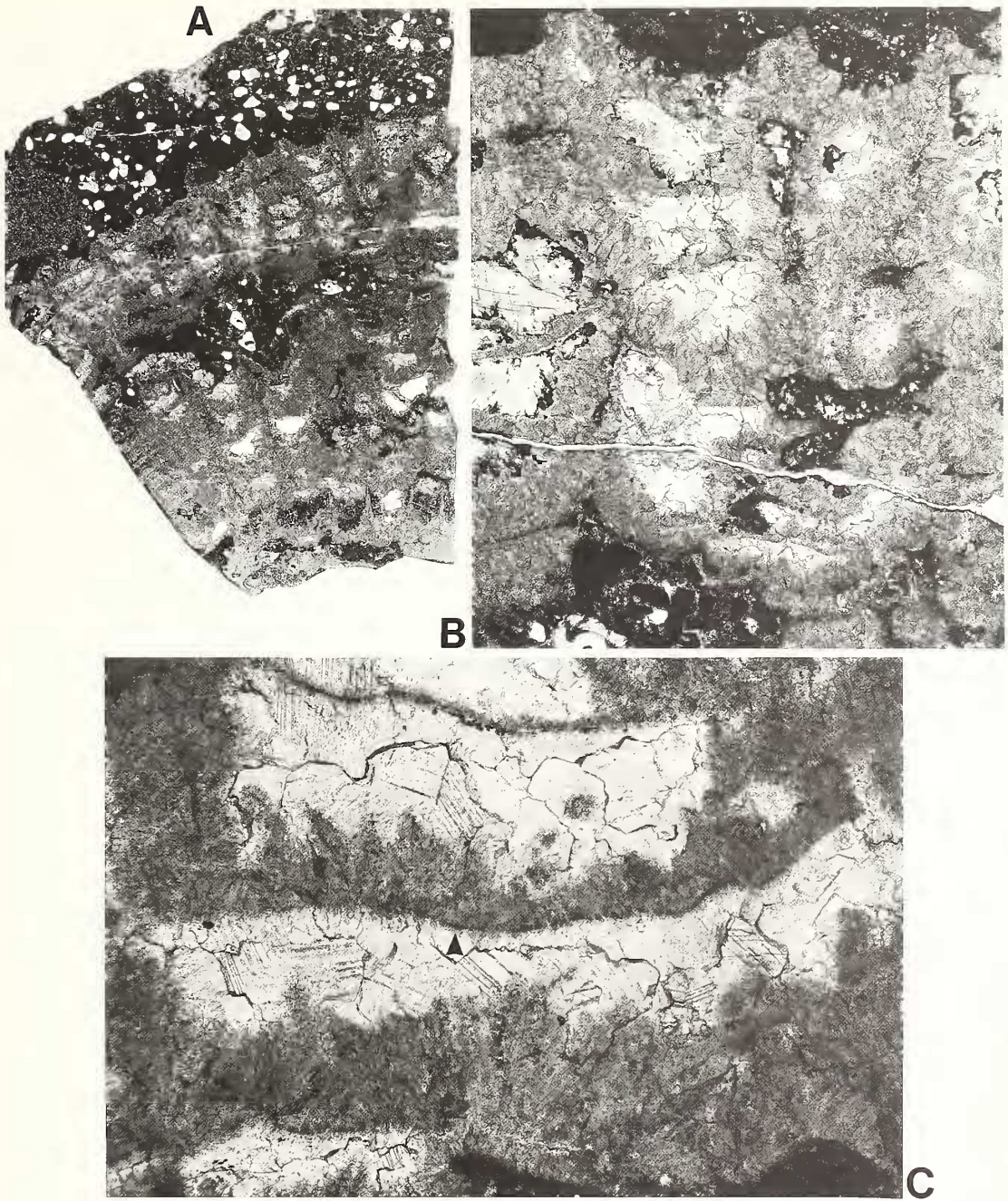
cerioid portions, ranging from 0.35 to 0.75 mm for one fibrous layer plus epitheca (Pl. 1, fig. 5). Wall thickness in cerioid corallites is difficult to measure, because fibrous, spherulitic growth is very luxuriant, and it is not always clear where the wall ends and the thick tabulae begin. Where thick walls are formed, outgrowths of spherulitic clusters of biogenic calcite continue into the corallite as nubs or spines (Pl. 2, figs 1–2). These spines are not as sharply developed, nor do they show the regularity of size, development or arrangement that is typical of septal spines in tabulates later in the Palaeozoic. The type specimen, illustrated by Fuller and Jenkins (1994, figs 2–5) has considerable development of septa (or septal spines), far more than seen in any of our specimens.

In cerioid parts of the corallum, stereozones in adjoining corallites are sometimes separated by red mud; in one, it was seen that the corallite wall was retracted after sediment had lodged between the skeleton and polyp (Pl. 1, fig. 5). Where large amounts of sediment are present within the corallum, individual corallites are separated from each other and are rounded, and corallite walls are much thinner than elsewhere in the corallum. Also, under these conditions, the inner wall or stereozone is thinner, with its fibrous structure formed by smaller, parallel-oriented crystals (Pl. 2, fig. 1). This contrasts with the fibres arranged in recognizable spherulitic clusters where growth was luxuriant in fully cerioid corallites (Pl. 2, fig. 3). Where corallite walls are thin adjacent to sediment, spinose projections on the walls more clearly resemble septal spines (Pl. 2, fig. 1).

In longitudinal section, tabulae are clearly seen to be composed of a basal dark layer and overlying spherulitic fibres (Text-fig. 5A–C). The tops of tabulae are uneven where tabulae are thick, with finger-like to spinose, upward-extending crystal growths. Walls are not always continuous vertical structures, as the fibrous layer of tabulae commonly merges with the stereozone of intercorallite walls (Text-fig. 5B).

Remarks. *Moorowipora chamberensis* shares more characters with cnidarian corals than does *Flindersipora*. It is truly cerioid (Pl. 1, figs 2–3), with mature corallites having maximum diameters near 4.5 mm. The tabulate-like features of this coral are as follows:

(1) The cerioid nature of intercorallite walls is typical of massive colonial corals of the Palaeozoic. This is seen where a tripartite wall (epitheca flanked by fibrous layers) separates cerioid corallites (Pl. 1, figs 2–3). The fibrous wall is either composed of slightly diverging crystal fibres of



TEXT-FIG. 5. *Moorowipora chamberensis*; all longitudinal sections; S.A.M. P34794. A, overview of corallum with straight corallites, abundant tabulae, and sediment encapsulated within colonial skeleton; $\times 2$. B, enlargement of upper portion of A, showing development of thick tabulae with fibro-normal structure; $\times 8$. C, structure of tabulae in second longitudinal thin section, here (arrow) showing thin 'dark line' at base of tabula and luxuriant upward growth of clusters of crystallites above; $\times 25$.

interfering spherulitic clusters or parallel calcite fibres normal to the flanks. This bilateral symmetry is regarded as a reflection of the individuality of cnidarian polyps. The skeleton-forming sponges typically do not have a cerioid wall, but rather, 'have a unitary microstructure' (Scrutton 1987, p. 488). Increase in *M. chamberensis* is lateral, as is typical for the Tabulata; this does not occur in the skeleton-forming sponges.

(2) The structure of the tabulae in the corallites is very similar to that in both tabulate and rugose corals occurring later in the Palaeozoic. The tabulae of this Lower Cambrian coral are formed of a thin, dense basal layer and an overlying thicker layer with upwardly oriented spherulitic crystallites forming the bulk of the tabula (Text-fig. 5B-C). This two-layered tabular structure in *Moorowipora* also strongly resembles that of *Tabuloconus* (Debrenne *et al.* 1987, p. 5), and is similar to that seen in later Palaeozoic corals (both Rugosa and Tabulata). This is the structure of dissepiments, the analogous platforms in modern Scleractinia. As shown by Wells (1969) and by Sorauf (1970) these develop by centripetal growth of fine crystallites to form the basal layer, prior to thickening by upward growth of interfering fibrous spherulites. This is very characteristic of coral skeletogenesis.

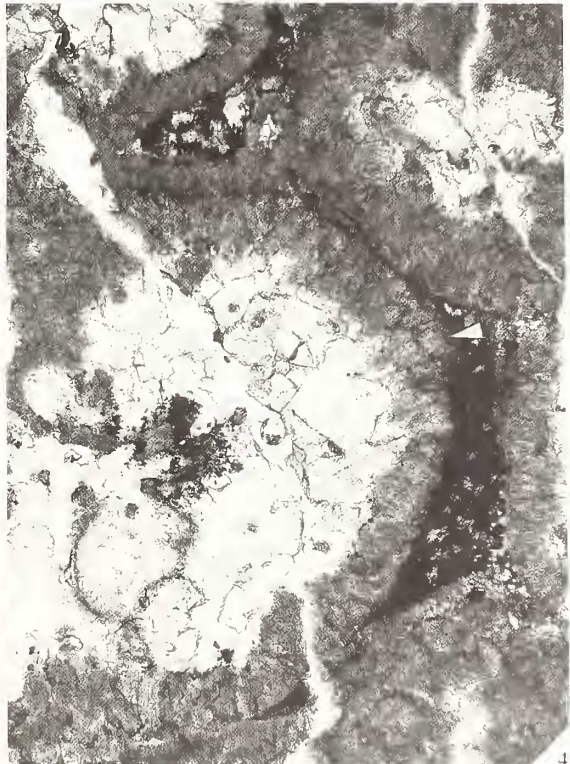
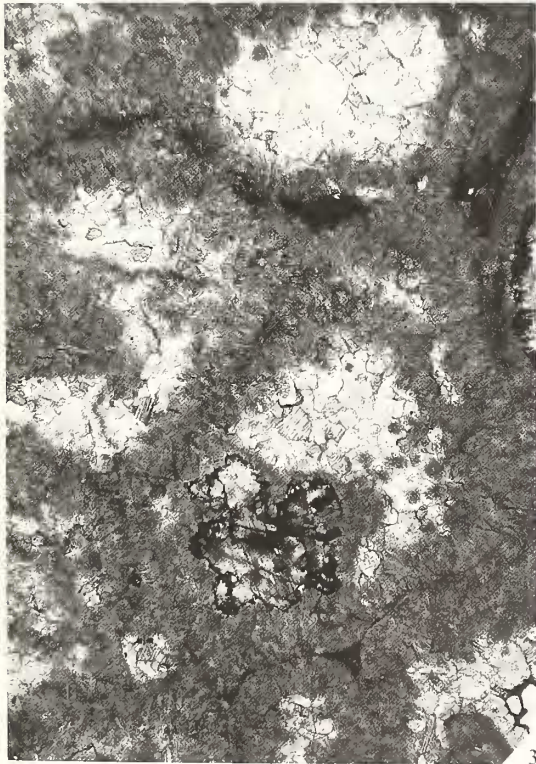
(3) Spines are seen as sharp protrusions on the inside of intercorallite walls, with bases which extend to the exterior surface of the wall (Text-fig. 5A). These do not resemble completely the septal spines of Tabulata, but suggest a similar origin, especially where walls are thin and spines are best defined. Hill (1981, p. F443) noted that septal spines are the most common septal elements seen in the Tabulata and indeed the type considered characteristic of the order.

(4) Another coralline characteristic is observed where terrigenous clastic sediment impinged on the colonies (Pl. 1, figs 1, 4-5). The subsequent contraction, and resultant isolation of individual polyps, led to formation of rounded, tubular corallites separated from one another by sediment. The development of gaps between corallite walls in the Tabulata is interpreted as having an environmental cause, and when they occur they are associated with sediment influxes and appear uniformly across much of the colony (Ross 1953, p. 40). The resulting subcerioid colonial form is commonly seen in Palaeozoic colonial rugose corals where influx of sediment caused retraction of polyps and allowed for sediment-filled spaces between corallites. These Lower Cambrian colonies later expanded laterally to cover this sediment, and the cerioid colonial form was resumed, thus encapsulating muddy red sediment within the corallum. Scrutton (1979, p. 182) noted that this is a typical reaction, and 'deposition by more or less individualized polyps' of skeleton is typical of cnidarians.

(5) The size and configuration of corallites most resembles those in mid-Palaeozoic Tabulata. *M. chamberensis* does not have mural pores as do the cerioid favositid tabulates, and the wall and tabular structure in places is more coarsely fibrous and spherulitic than later tabulate skeletons with their structure of parallel crystal fibres (Pl. 2, fig. 4). However, in *Moorowipora*, when corallites are round and walls are thin, the wall microstructure shows orderly, parallel crystallites (Pl. 2, fig. 1). Mural pores are regarded by Scrutton (1979, p. 182) as having been evolved by favositids later in the Palaeozoic, representing a more integrated colonial state than nonporous tabulate colonies. *M. chamberensis* also has spherulitic, trabecula-like prominences both within walls and on tabular floors (Text-fig. 5C). Development of these spinose projections by upward spherulitic growth of

EXPLANATION OF PLATE 2

Figs 1-3. *Moorowipora chamberensis*; all transverse sections; S.A.M. P34794. 1, corallites in contact with infiltrated clastic sediment, with fibro-normal wall structure and weakly developed septal spines (arrow); $\times 25$. 2, corallite with extreme rejuvenation (contraction) resulting from influx of clastic sediment. The fibrous nature of the corallite wall and beginnings of septal spines (arrow) is clearly shown; $\times 25$. 3, cerioid walls of corallites, fibrous wall structure and septal spines; $\times 10$. 4, cerioid part of corallum with small amount of clastic sediment infiltrated. Wall has pulled away from sediment, and wall structure is shown clearly to be composed of fibrous clusters of calcite crystallites (arrow); $\times 15$.



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crystals from the top surface of the tabulae may forecast the development of septa by spherulitic growth as septal trabeculae.

The gap in the geological record of fossil corals, between this occurrence and that of the oldest undisputed tabulate, *Lichenaria*, in the Lower Ordovician (Tremadoc, Ibexian; see Scrutton, 1984, p. 111) makes the placement of this coral in the Tabulata somewhat uncertain. However, it is certain that these organisms formed skeleton in ways very similar to those of younger Palaeozoic corals, utilized similar mineralogies, and reacted in similar ways to excessive sedimentation during polypal growth. It seems apparent to us that these are true corals, anthozoan cnidarians with skeletal morphology, at present best placed within the Tabulata.

SIGNIFICANCE OF THIS OCCURRENCE

There are a number of ramifications of an Early Cambrian first appearance for tabulate corals. Firstly, given the present criteria used to define the Subclass Tabulata, both *Moorowipora* and *Tabuloconus* could be included, thereby extending its stratigraphical range considerably. Secondly, the existence of Early Cambrian tabulates would require that coral phylogeny (Scrutton 1984; Pandolfi 1989; Zhuravlev *et al.* 1993) be re-evaluated. Skeletonized colonial corals in the Botomian necessitate an Early Cambrian or late Proterozoic ancestor for the group. Thirdly, the lack of coral involvement in reef building in other geographical areas during the Botomian and in the post-Botomian Cambrian world-wide needs to be explained. It is also possible that corals such as these are present elsewhere in the Lower Cambrian and have not yet been recognized. Lower Cambrian coralomorphs have been discovered recently in western Canada (Pratt 1991) and in western United States (Phillip Signor, pers. comm. 1993). A long hiatus in reef growth occurred after the Toyonian extinction (Debrenne 1991) with corals not participating until the early Ordovician.

In addition, the skeletal microstructure of *Moorowipora* has a bearing on the recognition of biogenic and diagenetic skeletal structures. The skeletal structure in *Moorowipora* is typical of many Palaeozoic tabulate corals, and raises the question of whether characteristic skeletal structures do exist in Palaeozoic corals. Zhuravlev *et al.* (1993) did not recognize fibrous skeletal structures in their scheme for radiation of the Lower Cambrian coralomorphs, and thus the occurrence of this type of wall in *Moorowipora* is of considerable significance in understanding early development of the cnidarian skeleton. *Moorowipora* can provide a model of a structural 'starting point' for development of Lower Palaeozoic Tabulata. Regardless of whether *M. chamberensis* is placed within the Tabulata, it should be agreed that these early Cambrian anthozoans were both cerioid and subcerioid in colonial form, and built skeletons in the same fashion as later tabulate corals that lack mural pores. *Moorowipora* and the Ordovician tabulate *Lichenaria* share the cerioid colonial form, fibrous intercorallite walls and presence of tabulae, and both lack mural pores. *Moorowipora* and *Tabuloconus* both have integral and individual corallites, fibrous wall structure, two-layered structure in tabulae, and are both here regarded as possible Tabulata. The presence of Lower Cambrian coral skeletons formed of calcite that was fibrous, spherulitic, and layered in similar ways to skeleton in later Palaeozoic corals indicates that coral-like biomineralization in the Cnidaria evolved first during the early Cambrian radiation, rather than in the Ordovician.

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